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Random Mating and Planktotrophic Larval Development in the Brooding Hermaphroditic Clam *Lasaea australis* (Lamarck, 1818)

by

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Abstract. *Lasaea australis* differs markedly from congeners in important details of its early ontogeny and reproduction. Adults brood their young to a straight-hinged veliger stage and an obligate planktotrophic larval period precedes settlement and metamorphosis. Several lines of evidence indicate that *L. australis* reproduces primarily by cross-fertilization. These include the maintenance of a Hardy-Weinberg-Castle equilibrium, and an observed heterozygosity level of 0.635, at the highly polymorphic glucose-6-phosphate isomerase locus. In addition, *L. australis* appears to be an alternate sequential hermaphrodite and has a large male allocation (approximately 50% in terms of gonadal volume). These results are the first to provide evidence of amphimixis in *Lasaea*. A profound dichotomy exists within the genus in developmental and reproductive modes, and population genetic structure. *Lasaea australis* probably represents the ancestral condition, and congeners that lack a planktonic larva form a complex assemblage of uncertain taxonomic status.

INTRODUCTION

The galeommatacean bivalve genus *Lasaea* is known from the Eocene period and has attained a near-cosmopolitan distribution (Chavan, 1969). *Lasaea* are small (≤6 mm in valve length) crevice dwellers, found in the rocky intertidal within cracks, algal holdfasts, barnacle test interstices, lichen tufts, and under rocks (Keen, 1938; Morton, 1954; Morton *et al.*, 1957; Oldfield, 1964; Glynn, 1965; Ponder 1971; Booth, 1979; Seed & O'Connor, 1980; Crisp *et al.*, 1983; Roberts, 1984; Beauchamp, 1986; McGrath & Ó Foighil, 1987). Although *Lasaea* is one of the better studied and most readily sampled marine bivalves, its taxonomy and some aspects of its reproduction are subject to conflicting interpretations.

Bivalve systematists have traditionally relied heavily on shell morphology to distinguish between species. There is much individual variation in *Lasaea* shells (Dall, 1900; Ponder, 1971; Roberts, 1984; Ó Foighil, 1986a; Ó Foighil & Eernisse, in press) and this poses a difficult taxonomic dilemma. Keen (1938) lists >40 species distinguished from each other on the basis of slight differences in shell morphology and color. A number of more recent workers, however, have been unable to separate many of these nominal *Lasaea* species (Soot-Ryen, 1960; Dell, 1964; Barnard, 1964; Ponder, 1971; Haderlie & Abbott, 1980; Beauchamp, 1985). An extreme alternative view is that the genus is monospecific (Dall, 1900; Lamy, 1906; Dautzenberg, 1929). Ponder (1971) concluded that many of the nominal *Lasaea* species are merely regional subspecies or ecotypes of the type species *Lasaea rubra* (Montagu, 1803). However, he distinguished two additional species, *L. australis* (Lamarck, 1818) and *L. maoria* (Powell, 1933), on the basis of shell and soft part morphology.

Population genetic studies of *Lasaea* in Europe (Crisp *et al.*, 1983) and the northeastern Pacific (Ó Foighil, 1986a; Ó Foighil & Eernisse, in press) have revealed the existence of a variety of non-hybridizing, frequently sympatric, genetic strains. These results have important implications for understanding morphological variation and systematic relationships within the genus. Crisp *et al.* (1983) concluded that the populations they examined were composed of female, apomictic clones. They apparently overlooked an earlier detailed study (Oldfield, 1961) which

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described European *Lasaea* as simultaneous hermaphrodites with greatly reduced male allocation, recently confirmed by McGrath & Ó Foighil (1986). Ó Foighil & Eernisse (in press) consider that northeastern Pacific *Lasaea* strains are either products of prolonged autogamy (self-fertilization), or pseudogamy in association with meiotic parthenogenesis.

Galeommatacean species investigated to date brood their young, either to a straight-hinged veliger (Chanley & Chanley, 1970; Ó Foighil & Gibson, 1984) or to a crawl-away juvenile stage of development (Gage, 1979). *Lasaea* developmental modes have been determined in European (Oldfield, 1964; Seed & O'Connor, 1980; McGrath & Ó Foighil, 1986), Ascension Island (Rosewater, 1975), New Zealand (Booth, 1979), Hawaiian (Kay, 1979) and northeastern Pacific (Glynn, 1965; Ó Foighil, 1986; Beauchamp, 1986) populations. In all of these cases, offspring are released as crawl-away juveniles. There are indications, however, that *L. australis*, which occurs around the Australian continent (Dell, 1964), may differ from its congeners in its developmental mode. Ponder (1971) reports that *L. australis* has a smaller prodissoconch (approximately 200 μm in length) relative to other *Lasaea* (500–600 μm). Prodissoconch size is directly related to egg size and developmental mode in eulamellibranch bivalves (Ockelmann, 1965; Waller, 1981; Jablonski & Lutz, 1983). The smaller *L. australis* prodissoconch is indicative of a shorter brooding period, possibly involving an obligate planktonic larval state. Roberts (1984) investigated the reproductive cycle of *L. australis* in Western Australia and described it as being larviparous, without reporting the developmental stage when released from the parent, egg size, or brood number. *Lasaea* that retain their young to a juvenile stage of development have also been frequently described as brooding "larvae" (Booth, 1979; Kay, 1979). Confirmation that *L. australis* does indeed differ in its developmental mode from other *Lasaea* is important because developmental modes exert a profound influence on population genetic composition and consequently on the evolution of reproductive patterns (Charlesworth & Charlesworth, 1981; Strathmann *et al.*, 1984; Lande & Schemske, 1985). Though there is yet no evidence for cross-fertilization in this genus, a reproductive mode involving an obligate larval dispersal is likely to result in high population genetic diversity (Berger, 1983) which would form a potent genetic penalty for self-fertilizers in the form of a pronounced inbreeding depression (Maynard Smith, 1978). Accordingly, an obligate planktonic larval period in *L. australis* should select for a predominantly cross-fertilizing reproductive mode.

The aim of this study is to assess the systematic status of *Lasaea australis* within this unusual genus by characterizing its developmental and reproductive modes. A live sample was obtained (courtesy of W. F. Ponder, Australian Museum), from which the hinge structure, duration of brood care, sex allocation, and population genetic structure at a polymorphic isozyme locus were determined.

MATERIALS AND METHODS

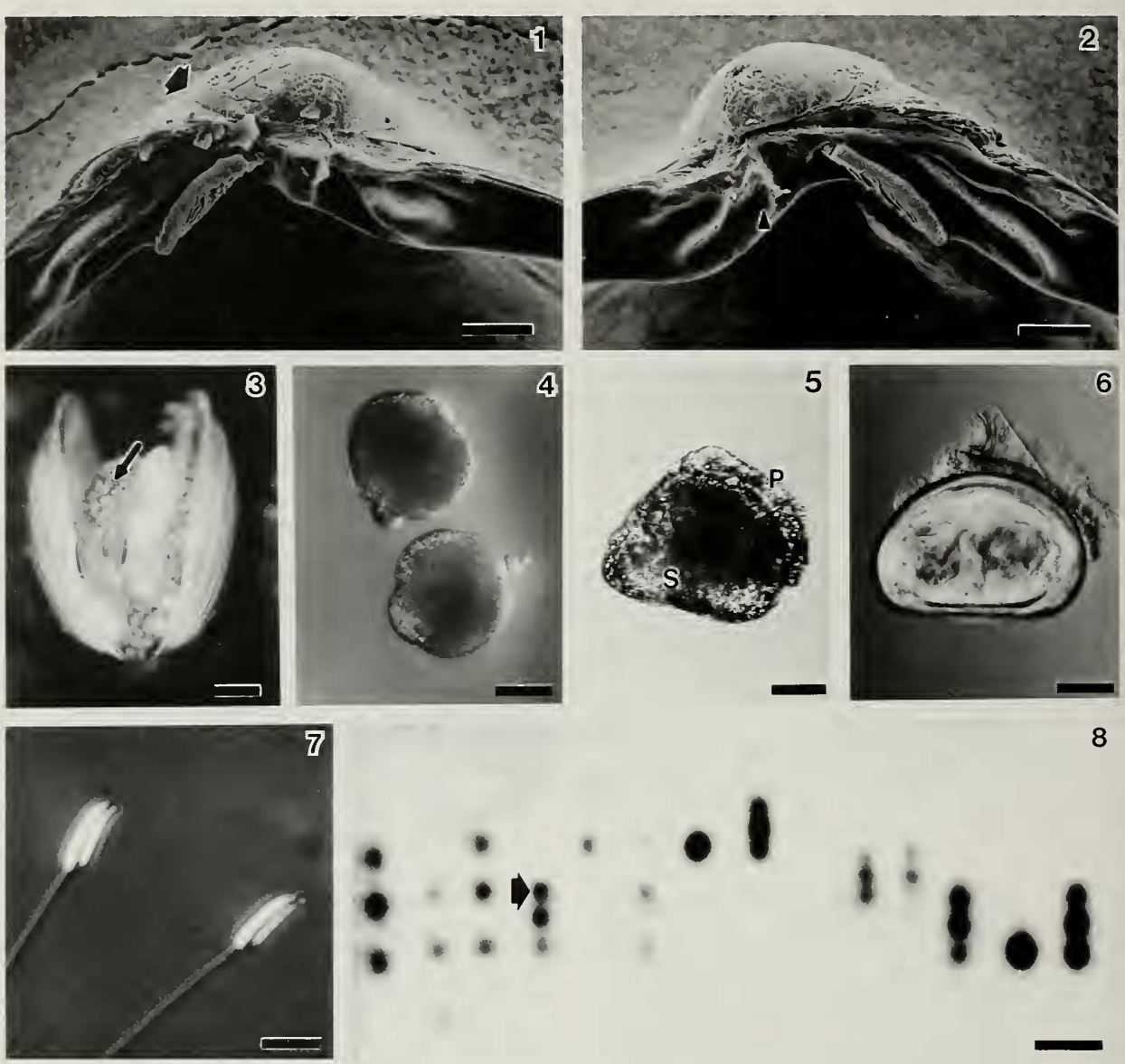
One hundred and five specimens of *Lasaea australis* were sampled in August 1987 from the intertidal zone at Long Reef, New South Wales, Australia (33°44′S, 151°18′E) by P. H. Colman. They were heat-sealed in a plastic bag containing approximately 50 mL of seawater, were air mailed, and arrived at the Friday Harbor Laboratories 10 days later. All specimens survived the trip; indeed, many had spawned en route and were brooding developing embryos upon arrival. They were maintained in seawater tanks at room temperature (18–20°C) and fed cultured *Thallassosira pseudonana* (strain 3H) for a week, then starved for one day before electrophoretic analysis.

Ninety-eight specimens were characterized electrophoretically using 13% starch gels and standard power supplies. Broods were dissected from reproducing individuals; the adults were then removed from their valves and homogenized with glass rods in an equal volume of gel buffer. A single discontinuous tris-citrate buffer system (electrode: 18.55 g boric acid and 2.4 g sodium hydroxide/L, pH 8.2; gel: 9.21 g tris and 1.05 g monohydrate citric acid/L, pH 8.7) was used. The following enzymes yielded monomorphic protein phenotypes: leucine amino peptidase, peptidase with glycyl-lycine, and peptidase with leucyl-valine and leucyl-tyrosine substrates. Glucose-6-phosphate isomerase (GPI; EC 5.3.1.9), however, produced closely migrating, polymorphic protein phenotypes, which were sufficiently resolved when gels were run at 200 volts until the front had reached a preset "destiny" of 130 mm. The GPI staining assay and method of scoring electromorph phenotypes of Tracey *et al.* (1975) were employed. Statistical analyses were performed using standard techniques as previously described (Ó Foighil & Eernisse, 1987).

Hinge structure of air-dried, gold-coated *Lasaea australis* valves was examined using a JOEL JSM-35 scanning electron microscope and compared with that of congeners from Victoria, B.C. (Canada), New Zealand (lots m. 21828 and m. 21011, National Museum of New Zealand), Japan (lot 78-14, Los Angeles County Museum of Natural History), Florida (lot PSM-743, Indian River Coastal Zone Museum), Britain (lot 35873, Museum of Zoology, University of Michigan), South Africa (lot A32355, South African Museum), and the Seychelles (lot 2222, British Museum of Natural History). Brooding individuals were photographed with a Wild Photomacroscope. Straight-hinged veliger larvae released by brooding parents were relaxed in 6.7% $MgCl_2$ at 4°C and fixed in 2% formaldehyde. Embryos, larvae, and sperm cells were photographed using Nomarski differential interference contrast optics on a Nikon Optiphot light microscope.

RESULTS

Figures 1 and 2 respectively show the hinge structure of the left and right valves of a *Lasaea australis* specimen 1.2 mm in valve length. The left hinge contains a single truncated anterior lateral tooth, a short thornlike cardinal (more



Explanation of Figures 1 to 8

Figure 1. Scanning electron micrograph (SEM) of left hinge of *Lasaea australis* specimen 1.2 mm in valve length. Arrow indicates prodissoconch-dissoconch boundary. Scale bar = 75 μm.

Figure 2. SEM of right valve of same *L. australis* specimen as in Figure 1. Arrow indicates small spur on posterior end of ventral anterior lateral tooth. Scale bar = 75 μm.

Figure 3. Light micrograph (LM) of a brooding *L. australis*, with opened valves, revealing brood mass (arrow) in the suprabranchial chamber. Scale bar = 0.5 mm.

Figure 4. Nomarski differential interference contrast (DIC) LM of *L. australis* eggs removed from the brood chamber just prior to first cleavage. Each egg bears polar bodies at the animal pole and a polar lobe at the vegetal pole. Scale bar = 40 μm.

Figure 5. Nomarski DIC LM of a *L. australis* larva dissected from the brood chamber at a late trochophore stage of development. Note developing shell (S) and faint prototroch (P). Scale bar = 30 μm.

Figure 6. Nomarski DIC LM of a *L. australis* straight-hinged veliger just after release from parent. The well-developed velum is partially retracted. Scale bar = 40 μm.

Figure 7. Nomarski DIC LM of *L. australis* sperm cells. Scale bar = 5 μm.

Figure 8. GPI electromorphs of 13 Long Reef *L. australis* individuals showing all five alleles detected in this study. Arrow indicates the modal allele (100). Scale bar = 10 mm and is placed anodally.

pronounced in larger specimens), an oblique resilium, and a lamellar posterior lateral tooth. In the right hinge, the short anterior lateral is bifurcate, forming a groove that accepts the left anterior lateral. In larger individuals this bifurcation is less evident and the ventral anterior lateral becomes much more pronounced, developing a spur at its posterior end which may represent a fused cardinal tooth (Figure 2). The right hinge also contains a pit which articulates with the left cardinal tooth, an oblique resilium, and two lamellar posterior laterals. The ventral posterior lateral is relatively more pronounced, and the groove separating the two laterals accepts the single posterior lateral of the left hinge. Shell shape, color, and sculpture are variable as previously found by PONDER (1971) and ROBERTS (1984). Individuals could be entirely white or pinkish-red in external valve coloration and many specimens had abruptly changed shell coloration during valve growth. Some individuals had heavy concentric folding on their external valve surfaces.

As in other *Lasaea,* developing young are retained in the suprabranchial chamber (Figure 3). The brood is held in both inner and outer demibranchs; the latter is reduced to one-third the size of the inner demibranch. Brood sizes of 440 and 2870 were produced by two individuals, 2.16 and 4.25 mm in respective valve lengths. *Lasaea australis* eggs are 90–95 μm in diameter and undergo two maturation divisions before first cleavage (Figure 4). Early development is similar to that found in other galeommatacean bivalves that retain their offspring to a straight-hinged veliger stage of development (Ó FOIGHIL & GIBSON, 1984). A shell is formed at the late trochophore stage and it gradually extends to cover a poorly developed prototroch (Figure 5). When released from the parent, the larvae are planktotrophic veligers (Figure 6) and have a mean length of 144 ± 3.9 μm SE ($n = 15$). *Lasaea australis* prodissoconch morphology is typical of bivalves with planktotrophic development (OCKELMANN, 1965; CARRIKER & PALMER, 1979; WALLER, 1981; JABLONSKI & LUTZ, 1983; Ó FOIGHIL, 1986b). Newly metamorphosed juveniles possess an umbonate hinge line, a small prodissoconch-I (130–150 μm in length) and have a mean length of 249 ± 19.6 μm SE ($n = 10$), based on prodissoconch-II measurements.

Specimens brooding early embryos did not retain any residual vitellogenic oocytes in the gonad and had obviously just spawned as females. However, the testes of these individuals were usually full of mature sperm (7 out of 9 cases). These data imply that *Lasaea subviridis* is a sequential alternate hermaphrodite, although observations of actual spawnings are necessary to confirm this. Male allocation in *L. australis* is considerable, being roughly equal to female allocation in terms of gonadal volume. *Lasaea australis* sperm morphology at the light microscope level conforms to the "primitive" sperm type found in most externally fertilizing aquatic organisms (FRANZÉN, 1956; AFZELIUS, 1972). The sperm heads contain a fully condensed nucleus and are uniform in shape and size (Figure 7).

Table 1

Allelic frequencies of Long Reef *Lasaea australis* at the GPI locus.

Allele	Frequency ± 1 SE
82	0.0306 ± 0.0123
92	0.3367 ± 0.0337
100	0.3673 ± 0.0344
108	0.2449 ± 0.0307
114	0.0306 ± 0.0123

Ne (effective number of alleles) = 3.225. Number of alleles screened = 196. Observed proportion of heterozygotes (Ho) = 0.653. Expected proportion of heterozygotes (He) = 0.690. D = −0.053 when D = (Ho − He)/He (SELANDER, 1970).

GPI electromorphs from the 98 individuals analyzed for this enzyme consisted of either one or three bands (Figure 8), indicating that this enzyme has a dimer subunit structure in *Lasaea australis*. The protein phenotype combinations observed are consistent with the hypothesis that five distinct alleles segregating through a single locus were distinguished. Therefore, single-banded individuals were assumed to be homozygous and three-banded animals heterozygous at the GPI locus. Allele frequencies and genotype distributions are presented in Tables 1 and 2 respectively. The calculated D value (SELANDER, 1970) of −0.053 is marginally less than the expected value of 0 and indicates that there is a slight deficiency of heterozygotes at the GPI locus. However, the observed allele combination frequencies do not differ significantly from random mating expectations ($0.75 < P < 0.9$).

DISCUSSION

Lasaea australis differs from all congeners studied to date in important features of its reproductive and developmental biology. The maintenance of a Hardy-Weinberg-Castle equilibrium at the GPI locus ($0.75 < P < 0.9$) indicates that random mating occurs in the Long Reef population and provides the first evidence for cross-fertilization in this genus. Occasional self-fertilization by *L. australis* cannot be excluded; however, the observed GPI locus heterozygosity level of 0.653 suggests that, if it occurs, it is a rare event. Frequent self-fertilization would lead to a rapid drop in heterozygosity at all loci in the genome (SELANDER & KAUFMAN, 1973; BELL, 1982; BUCKLIN *et al.*, 1984).

Additional evidence for an amphimictic reproductive mode is provided by the large male allocation, approximately 50% of gonad volume, which is theoretically consistent with an outcrossing reproductive mode (HEATH, 1979; FISCHER, 1981; CHARLESWORTH & CHARLESWORTH, 1981; CHARNOV, 1982). European (OLDFIELD, 1964; MCGRATH & Ó FOIGHIL, 1986) and northeastern Pacific (Ó FOIGHIL, 1985a; BEAUCHAMP, 1986) *Lasaea* populations are composed of simultaneous hermaphrodites, the male allocation of which is approximately an

Table 2

Genotype distributions of the three most common GPI alleles of Long Reef *Lasaea australis*.

Genotype	Observed frequency	H-W-C expected frequency
92/92	11	11.110
92/100	26	24.239
92/108	13	16.162
100/100	14	13.221
100/108	13	17.631
108/108	9	5.878

$G = 0.88387$, df = 3, $0.75 < P < 0.9$ when G is the Log Likelihood Ratio.

order of magnitude smaller than that of *L. australis*. Sperm morphology is also different in *L. australis* in that sperm nuclei are fully condensed, resulting in a sperm head that is uniform in size and form. In European and northeastern Pacific *Lasaea* populations the degree of sperm nuclear condensation and the sperm head size and shape are variable (Ó Foighil 1985a; McGrath & Ó Foighil, 1986).

Data from the present study on early development of *Lasaea australis* confirms Robert's (1984) description of this species as being larviparous. *Lasaea australis* differs in its developmental mode from congeners in Europe (Oldfield, 1964; Seed & O'Connor, 1980; McGrath & Ó Foighil, 1986), the northeastern Pacific (Glynn, 1965; Ó Foighil, 1986; Beauchamp, 1986), Ascension Island (Rosewater, 1975), New Zealand (Booth, 1979), and Hawaii (Kay, 1979) in that it releases its young as straight-hinged planktotrophic veligers rather than as crawl-away juveniles. *Lasaea australis* has a correspondingly smaller egg size, greater fecundity, and assumes a benthic juvenile existence at a smaller size than congeners (McGrath & Ó Foighil, 1986).

The hinge structure of *Lasaea australis* is very similar to that of congeners from Victoria, B.C. (Canada), New Zealand, Japan, Florida, Britain, South Africa, and the Seychelles. Congeners, however, exhibit great individual variation in the degree of tooth development, especially that of the anterior laterals (Ó Foighil, unpublished data). This variation is much less pronounced in *L. australis*. *Lasaea australis* is readily distinguished from congeners by its larger size (up to 6 mm in valve length), presence of heavy concentric ridges on the external shell surface of some individuals, and smaller prodissoconch (Ponder, 1971).

Electrophoretic characterization of European (Crisp *et al.*, 1983) and northeastern Pacific (Ó Foighil, 1986; Ó Foighil & Eernisse, unpublished data) populations has revealed a variety of non-hybridizing, sympatric strains to whom species rank cannot yet be assigned with certainty. The profound differences in reproduction, development, and population genetic structure between *Lasaea australis* and its congeners, in addition to shell characteristics (Ponder, 1971), justify its ranking as a distinct species.

Available data on the population genetic structure, reproduction, and development of *Lasaea* reveal a prominent dichotomy between *L. australis* and European/northeastern Pacific populations (Crisp *et al.*, 1983; Ó Foighil, 1986; Ó Foighil & Eernisse, in press). *Lasaea australis* is a randomly mating species with an obligate planktotrophic larval development. The other *Lasaea* populations are composed of frequently sympatric, reproductively isolated strains, with no evidence as yet for cross-fertilization, and brood to a crawl-away juvenile stage of development. This population genetic structure can result from a variety of reproductive modes, including prolonged autogamy and apomixis (Bell, 1982).

Northeastern Pacific *Lasaea* are simultaneous hermaphrodites (Glynn, 1965; Beauchamp, 1986) with minute male allocation, approximately 5% in terms of gonadal volume (Ó Foighil, 1985a), and are capable of reproducing in isolation, apparently by self-fertilization (Ó Foighil, 1987). Reduced male allocation in simultaneous hermaphrodites is a theoretical consequence of high degrees of autogamy (Heath, 1979; Fischer, 1981; Charlesworth & Charlesworth, 1981; Charnov, 1982). Indeed, the population genetic structure of northeastern Pacific *Lasaea*, together with the ability to reproduce in isolation, a minute male allocation, and an apparent absence of specialized sperm transfer mechanisms typically found in cross-fertilizing brooding bivalves (*e.g.*, spermatophores and spermatozeugma [Coe, 1931; Ockelmann & Muus, 1978; Ó Foighil, 1985b], dwarf and complemental males [Turner & Yakovlev, 1983; Ó Foighil, 1985c] and pseudocopulation [Townsley *et al.*, 1965]) imply that cross-fertilization may be a very rare event in northeastern Pacific *Lasaea* populations (Ó Foighil, 1986a; Ó Foighil & Eernisse, unpublished data). The conclusion that northeastern Pacific *Lasaea* reproduce predominantly by autogamy (Ó Foighil, 1986a, 1987; Ó Foighil & Eernisse, in press) is supported by the marked difference in their population genetic structure and male allocation to that of the predominantly amphimictic *L. australis*. An alternative, less parsimonious interpretation is that northeastern Pacific *Lasaea* engage in a combination of pseudogamy and meiotic parthenogenesis (Ó Foighil, 1987). An analysis of the degree of male and female pronuclear interaction is necessary to distinguish between these two possibilities. European *Lasaea* populations are very similar in population genetic structure, male allocation, and presumably reproductive mode to northeastern Pacific *Lasaea* (Oldfield, 1961; Crisp *et al.*, 1983; McGrath & Ó Foighil, 1986).

A strong unidirectional bias exists in the transition between feeding and non-feeding larval development in marine invertebrates because loss of planktotrophy is usually accompanied by an extensive loss of larval feeding structures (Strathmann, 1978, 1985). Oldfield (1964) in-

terpreted the unciliated "cephalic mass" of *Lasaea rubra* embryos as a velum highly modified for yolk storage. Similar, though less developed, modifications in velar morphology are found in *Thyasira gouldi* and *Cardiomya pectinata* which lack feeding larvae (Blacknell & Ansell, 1974; Gustafson *et al.,* 1986). It is probable that the *Lasaea australis* developmental mode represents the primitive condition in the genus.

Loss of a dispersive life-history stage gives rise to philopatric dispersal patterns which can result in prolonged inbreeding (Jacquard, 1975). A history of inbreeding predisposes populations to the development of autogamy by removing recessive deleterious alleles (Charlesworth & Charlesworth, 1981; Charnov, 1982; Strathmann *et al.,* 1984; Uyenoyama, 1986). Self-fertile hermaphrodites with reduced male allocation appearing in these populations are then at a reproductive advantage because of their greater reproductive efficiency (Maynard Smith, 1978; Charnov, 1982; Strathmann *et al.,* 1984). The model of Strathmann *et al.* (1984) for the evolution of self-fertile hermaphrodites in marine invertebrate brooders that release crawl-away young may apply to all *Lasaea* populations that brood to this ontogenic stage. Once evolved, a completely self-fertilizing reproductive mode may be irreversible owing to a genetic advantage resulting from the "cost of meiosis" (Bull & Charnov, 1985).

Although amphimixis has for a long time been regarded as a preadaptation to variable conditions, comparative evidence shows that alternative reproductive mechanisms, including autogamy and apomixis, predominate in harsh and disturbed environments (Bell, 1982). The small size, physiological toughness, and behavioral adaptations of European (Ballantine & Morton, 1956; Morton *et al.,* 1957; Morton, 1960; Davenport & Beard, 1988) and northeastern Pacific (Glynn, 1965) *Lasaea* enable them to survive in their upper intertidal habitat. Prominent theories concerning the evolution and persistence of amphimixis, such as the Tangled Bank (Bell, 1982) and the Red Queen (Jaenike, 1978; Bell, 1982), stress its role in generating the genetic diversity necessary to endure in, and more fully exploit, biologically diverse environments. *Lasaea australis* not only differs from its congeners in reproductive mode, but also in habitat, occurring in the more biologically complex lower intertidal zone (Roberts, 1984).

A profound taxonomic dichotomy exists in the genus *Lasaea* that may have evolved as follows. Originally, the genus was composed of amphimictic hermaphrodites with an obligate planktotrophic larval development. To date, the only species known to retain this presumably ancestral condition is *L. australis.* Loss of a planktonic larva in some species led to the successful development of a self-fertilizing reproductive mode. It is not yet certain if self-fertilization has been maintained in northeastern Pacific populations, or if it has been replaced by a form of pseudogamy in which endogenous sperm trigger meiotic parthenogenesis. The absence of amphimixis has resulted in the formation of a complex of non-hybridizing, often sympatric strains in at least northeastern Pacific (Ó Foighil, 1986, Ó Foighil & Eernisse, in press) and probably in European (Oldfield, 1961; Crisp *et al.,* 1983; McGrath & Ó Foighil, 1986) populations. Taxonomic relationships among *Lasaea* that lack a planktonic larva are still poorly understood, but are undoubtedly complex (Ponder, 1971; Crisp *et al.,* 1983; Ó Foighil, 1986; Ó Foighil & Eernisse, unpublished data). Resolution of these relationships will require a multidisciplinary approach, applied to a variety of populations of this near-cosmopolitan genus.

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